FINAL REPORT

Impacts of historical disturbance regimes on avian conservation in eastern tallgrass prairies

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List of Abbreviations/Acronyms

A: chance-corrected within agreement statistic
AIC: Akaike’s Information Critereon
CMP: Conway-Maxwell Poisson
GLM: generalized linear model
GLMM: generalized linear mixed model
GRIN: Graduate Research Innovation
JFSP: Joint Fire Science Program
MRPP: multi-response permutation procedure
NMDS: non-metric multidimensional scaling
p: p-value
R: R statistical software
SD: standard deviation
SE: standard error
VIF: variance inflation factor
β: beta value

Keywords

bison
disturbance
grassland birds
grazing
prescribed fire
pyric herbivory
restoration
tallgrass prairie
vegetation structure

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Abstract

Grazing from native herbivores such as bison (*Bison bison*), in combination with prescribed fire, are applied to tallgrass prairies by managers to recreate important disturbance regimes in this ecosystem. Bird communities may be indirectly impacted by these disturbances, as bison and prescribed fire alters the structure of critical breeding habitat for grassland birds. The objectives of this research are to determine the impacts that bison and prescribed fire have on grassland breeding birds in two tallgrass prairie preserves, Kankakee Sands and Nachusa Grasslands. After slight adjustments to methods, and through the complexity and hurdles of the Covid-19 pandemic, the objectives of this research were met. Bird communities, vegetation structure, and bison activity were surveyed systematically at these two preserves in 2020 and 2021. Prescribed fire histories were derived from management records at both preserves. We used multivariate analyses to examine the differences in bird community composition between categorical disturbance types, survey year, and preserve location. Additionally, bird richness and focal grassland obligate species abundances were analyzed using generalized linear mixed models to determine the impact of disturbance, management, and vegetation variables. We found that disturbance regime type impacted bird community composition more than interannual variation or preserve location. Bird species richness was highest within management units that were unburned, regardless of bison presence, in comparison to burned units without bison. Vegetation structure had the largest impact on grassland obligate bird abundances, with grazing and fire disturbances having larger impacts than restoration planting age and spatiotemporal factors. We found that pyric herbivory impacted two grassland obligate species, Dickcissels (*Spiza Americana*) and Henslow's Sparrows (*Centronyx henslowii*), that showed varying abundances when bison and fire interacted. Specifically, Dickcissel abundance decreased with years since fire, but this decrease was lessened when bison were present. Additionally, Henslow's Sparrow abundance increased with years since fire, with a more pronounced increase when bison were present. These results highlight the importance of applying varying levels of grazing and fire disturbance in order to provide a heterogeneous landscape with variable vegetation structure to accommodate the life history preferences of a diversity of grassland bird species. Species-specific preferences of disturbance intensity and vegetation structure may be used to manage for particular species of conservation concern at these preserves and throughout the region.

Objectives

The original objective of this thesis research prior to application to this Graduate Research Innovation (GRIN) Award was to determine the impacts that reintroduced bison have on grassland breeding bird density and diversity throughout the three preserves that support wild bison in eastern tallgrass prairies. Additional objectives added to this thesis research upon application and acceptance of the GRIN proposal were to determine the impacts that prescribed fire and the combined impact of fire and bison disturbance have on grassland breeding birds in eastern tallgrass prairies. Modifications to the studies methods as indicated in the April 2021 progress report changed the scope of the project from three preserves to two preserves with the removal of Midewin Grasslands from the studies research sites. We predict that bird community composition will be impacted by differing disturbance regimes following the intermediate disturbance hypothesis, with intermediate levels of disturbance yielding higher bird richness (Grime 1973, Connell 1978). Additionally, we predict that bird species abundances will be impacted by disturbances through changes in vegetation structure, based on life history and breeding habitat requirements (Figure 1). Specifically, we predict species like Henslow's Sparrow will have higher abundances in unburned and ungrazed sites, while species like Grasshopper Sparrow will have higher abundances in burned and grazed sites.

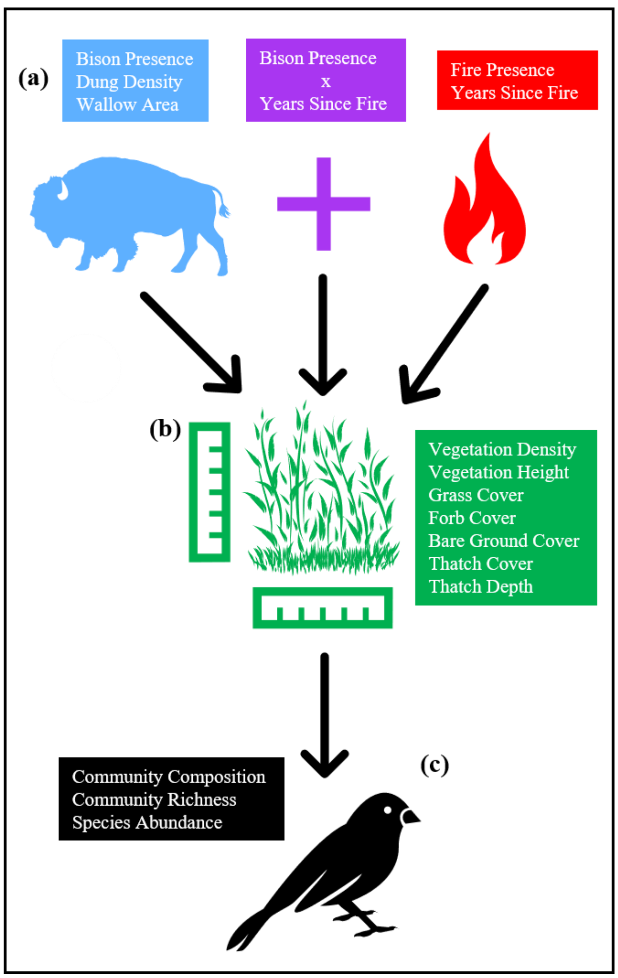

Figure 1. Conceptual figure depicting the hypothesized interaction and impact of bison and fire disturbance on grassland birds, (b) through the medium of vegetation structure. Variables included in hierarchical models are listed and separated by section: disturbance variables (a), vegetation structure variables (b), and bird community and abundance variables (c).

These objectives relate directly to the topic of “fire effects and post-fire recovery”, while also supporting the goal of “fire-adapted communities” from the 2014 National Cohesive Wildland Fire Management Strategy. Funding from this GRIN Award successfully enhanced the quality and scope of this thesis research by providing an avenue to collect more data through the hiring of two field technicians. This also gave the student researcher critical experiences in developing a job posting, interviewing, hiring, developing safety protocols, training research techniques, and supervising. Additionally, this funding encouraged increased interactions with fire and natural resources managers to better determine the informational and research needs at these two preserves. Thus, the objectives of the study took on a more management and policy relevant focus, in addition to the theoretical focuses that the research was originally founded upon.

Background

Tallgrass prairie is one of the world’s most endangered biomes, with an estimated 0.1 percent of its historical extent remaining in Illinois and Indiana, largely due to conversion of land to agriculture and urbanization (Samson and Knopf 1994, Robertson et al. 1997). Concomitantly, grassland birds are declining in population faster than any other guild of birds in North America, with 70 percent of grassland bird species showing significant declines since the 1970s (Rosenberg et al. 2019). Along with conservation of remnant prairie, prairie restoration has become a critical strategy to restore the loss of biodiversity in an otherwise ecologically barren agricultural landscape. The recent declines in bird populations in North America along with the overall loss of tallgrass prairie habitat, signify that grassland birds are at risk and require conservation attention from the scientific community (Samson and Knopf 1994, Rosenberg et al. 2019). Within this patchwork of agricultural and urban landscapes, large tallgrass prairie preserves provide critical migratory and breeding habitat for these declining bird species. Management techniques such as prescribed fire and reintroduction of native grazers are being used in these preserves to restore historical disturbance regimes that have been absent from the landscape and are critical to the maintenance and integrity of tallgrass prairie ecosystems (Anderson 2006, Bach and Kleiman 2021). Therefore, it is important to understand the impacts that management techniques in these rare habitats have on grassland birds.

Disturbances via native herbivore grazing and periodic fire are important historical and current aspects of tallgrass prairie ecology. Indigenous communities were the original stewards of this ecosystem, shaping tallgrass prairies through setting fires and utilizing American bison (Bison bison) and other natural resources as a way of life (Kimmerer and Lake 2001, Roos et al. 2018, Robinson et al. 2021). However, bison were driven to near extinction in the late 1800s due to commercial hunting and United States expansion policies aimed at removing Indigenous communities (Hornaday 1889, Gates et al. 2010). Today, managers seek to mimic these historical disturbances, similar to Indigenous methods, through the reintroduction of bison and prescribed fire application. Bison historically played an ecologically important role in North American prairie ecosystems by affecting biodiversity and ecosystem functioning through herbivory, wallows (bare patches created by rolling on the ground), and nutrient cycling (Knapp et al. 1999). Along with bison grazing, prescribed fire regimes are a critical component of maintaining tallgrass prairie habitat by reducing woody plants and recycling nutrients into the soil (Abrams and Hulbert 1987, Howe 1994, Bowles and Jones 2013). By restoring both native grazing and fire regimes, land managers attempt to restore pyric herbivory, the historical spatiotemporal interactions of these two disturbance regimes (Collins et al. 1998, Fuhlendorf et al. 2009, Hovick et al. 2015). Fire and bison, together and in isolation, create disturbances that are distributed unevenly across the landscape (Vinton et al. 1993, Fuhlendorf et al. 2009). This variation in disturbance will have an impact on vegetation structure, which may degrade or improve bird habitat depending on the intensity of disturbance at a given location and species-specific preferences (Grime 1973, Connell 1978, Shea et al. 2004).

The environmental context and successional trajectory of restored tallgrass prairies in Illinois and Indiana differ from the western tallgrass prairies from which much of our knowledge is derived. Restored prairies in these eastern states are mosaics of different restoration ages, yielding varied plant communities which might be preferred differentially by bison (Blackburn et al. 2021). Moreover, these tallgrass prairies are smaller in area, more isolated, and receive more precipitation than better-studied western tallgrass prairies which provide more contiguous habitat and drier climate (Samson and Knopf 1996, Samson et al. 2004). Managers have reintroduced bison to eastern tallgrass prairies in recent years (2014-2016), in contrast to bison that were reintroduced in 1987 and 1993 to Konza Prairie in Kansas and the Tallgrass Prairie Preserve in Oklahoma, respectively (Coppedge et al. 1998b, Knapp et al. 1999). One study from Illinois found a lack of response of birds to bison disturbances immediately following reintroduction, highlighting a potential time lag in bison impact on the landscape (Herakovich et al. 2021). Overall, the differences in climate, habitat, spatial context, and bird communities between western tallgrass prairies and eastern tallgrass prairies underscore the importance of studying grassland bird responses to differing disturbance regimes in this region to inform management decisions about bison and prescribed fire.

Materials and Methods

Study Area

The study was conducted at two eastern tallgrass prairies owned and managed by The Nature Conservancy – Nachusa Grasslands in Illinois and Kankakee Sands in Indiana (Figure 2). Both preserves contain chronosequences of restored tallgrass prairies, sections of prairie that were restored with similar methods and have similar characteristics, but differ in age. These restored prairie patches are connected to smaller patches of remnant prairie and savanna habitat, creating a mosaic of prairie-savanna habitat that totals ~1600 hectares for Nachusa Grasslands and ~3400 hectares for Kankakee Sands. Bison were reintroduced to a portion of both Nachusa Grasslands and Kankakee Sands in 2014 and 2016, respectively. A herd of approximately 115 bison were contained within a fenced unit of 506 hectares year-round at Nachusa Grasslands during the study period. At Kankakee Sands, the bison herd was approximately 100 bison during the study period and are fenced within two separate units. Sampling was conducted in the summer unit (303 hectares) where bison are contained from February to September. Managers at both sites use prescribed fire variably across the preserves. We were interested in researching the variable impacts of prescribed fire as they are implemented by site-specific managers, and therefore did not experimentally control where fire was applied during the study period but used it as a treatment in a natural experiment.

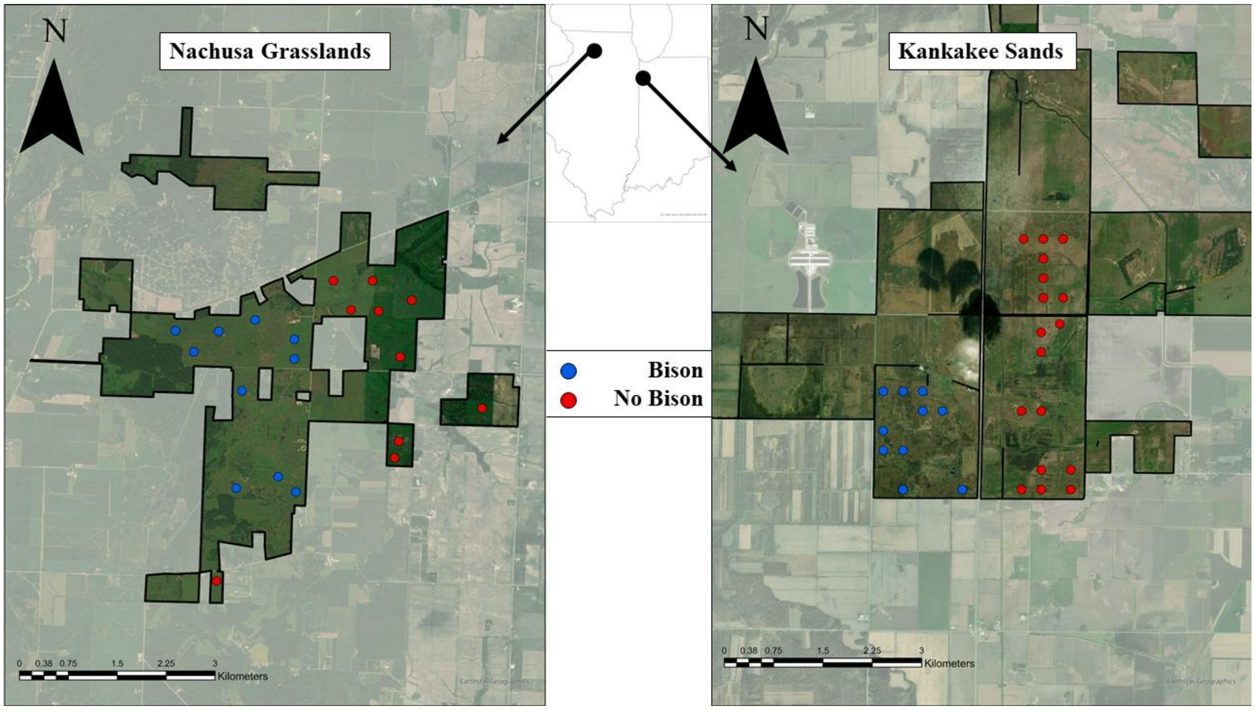

Figure 2. Map of survey plots within two tallgrass prairie preserves managed by The Nature Conservancy: Nachusa Grasslands, Illinois (left) and Kankakee Sands, Indiana (right). Plots are colored according to bison presence with blue circles representing plots within management units containing bison and red circles representing plots within management units without bison.

Data Collection

We selected survey plots within areas of high-quality tallgrass prairie, as defined by site managers, both within and outside of bison units and data were collected across two field seasons (2020-2021) (Figure 2). Survey plots were located greater than 300 meters away from adjacent plots. We quantified management variables such as time since fire and planting age for each survey plot using existing data provided by site managers at each preserve. In 2020, plots were evenly distributed between bison and non-bison units, with seven plots in each preserve/unit combination, totaling 28 plots. Prescribed fire application in 2020 was greatly reduced due to the restrictions related to the Covid-19 pandemic. In 2021, 19 additional plots were surveyed (total = 47) to help balance sampling effort among different disturbance types.

We surveyed bird species using 100-meter fixed radius point counts (Bibby et al. 2000). Surveys were repeated at each plot at least four times each season with surveyors identifying all birds seen and heard within a five-minute timeframe. Point counts were conducted during the last week of May through the first week in August each survey year to survey peak bird breeding season (late May-early July), while also surveying for species of concern with known breeding activity during the late summer (e.g. Sedge Wren) (Schramm et al. 1986, Bedell 1996). We conducted point counts during peak bird activity between 0515 and 1000 hours CDT, with survey start times and order being conducted randomly within this timeframe. Surveys were not conducted during periods of rain or strong winds.

We surveyed vegetation structure at each plot from late-May to early-August along four 100-meter transect lines in each cardinal direction from plot centers. Vegetation cover was surveyed following standard sampling procedures (Daubenmire 1959). Visual obstruction readings (hereafter referred to as vegetation density), vegetation height, and dead plant litter (hereafter referred to as thatch) depth were measured following standard sampling procedures (Robel et al. 1970, Ahlering and Merkord 2016). Vegetation structure surveys were conducted three times per field season to capture the differences in vegetation structure throughout the growing season.

We surveyed two variables as proxies for bison disturbances on the landscape. Bison dung was surveyed as a proxy for bison activity at a given plot by counting bison dung piles within one meter of transect lines (Milchunas et al. 1989, Barnes 2001). Bison dung was surveyed twice each field season to capture any within season variation. Additionally, bison wallows within a 100-meter radius of each plot were counted and measured in 2021 by measuring the largest and smallest diameter of each wallow to approximate the area.

Data Analyses

All data were analyzed in R statistical software version 4.1.2 (R Core Team 2021). To directly test for the impact of disturbance on bird community richness, we analyzed within-plot species richness for all observed species against categorical and continuous disturbance variables using linear mixed models. A nested random variable for study year, preserve, and plot was included within regression models to account for spatiotemporal autocorrelation.

Multivariate data was prepared by removing large ranging species (e.g. hawks and swallows) and species detected in less than five percent of study plots following standard procedures (McCune and Grace 2002, Zimmerman 1992,1997) We analyzed differences in bird community composition by year, preserve, and disturbance type using non-metric multidimensional scaling (NMDS) ordination plots. NMDS plots were derived from a Bray-Curtis dissimilarity matrix of species mean counts per survey plot per year. We then quantified differences in bird community composition by year, preserve and disturbance type using a multi-response permutation procedure (MRPP) with a Bray-Curtis dissimilarity matrix (Mielke 1984, Warton et al. 2012).

To test for the impact of disturbance on individual grassland-obligate breeding species, we analyzed the relative abundances (hereafter referred to as abundances) of five obligate grassland species for which we had enough point count data to conduct analyses: Dickcissel, Eastern Meadowlark, Grasshopper Sparrow, Henslow’s Sparrow, and Sedge Wren. First, coefficients were explored to identify outliers, correlation, collinearity, and necessary transformations (Steuter and Hidinger 2018, Zuur et al. 2010). Forb cover and vegetation height were correlated with grass cover and vegetation density, respectively, and were removed from global models. Thatch cover exceeded the collinearity threshold and was removed from the Henslow’s Sparrow global model. These coefficients were removed based on preference or interest in the retained coefficient, but we consider these variables when interpreting our results.

Following data exploration, we analyzed focal bird species abundances using generalized linear mixed models (GLMMs) fit with a poisson distribution to account for count data and included a nested random variable for study year, preserve, and plot for all species and a random variable for julian date when deemed necessary (Zuur and Ieno 2016). Models that tested for significant under-dispersion were fitted with a Conway-Maxwell Poisson (CMP) distribution to account for under-dispersion (Conway and Maxwell 1962, Shmueli et al. 2005, Lynch et al. 2015). Models fit with a CMP distribution were compared with the same model fit with Poisson distributions using Akaike's Information Criterion (AIC) to confirm model fitness (Zuur et al. 2009). To directly test the impact of differing disturbance regimes on bird abundances, we first ran GLMMs with disturbance as a categorical variable. We then analyzed the impact of other disturbance and vegetation structure variables through a hierarchical modeling framework (Burnham and Anderson 2002, Zuur et al. 2009, Harrison et al. 2018).

Results and Discussion

We identified 79 species of birds from surveys conducted in 2020 and 2021. Of these total species, we included 27 species in the multivariate analyses following our protocol in the methods (Table 1). Focal grassland bird species combined abundance accounted for about 50 percent of total bird abundance observed during the study period.

Table 1. Four-letter alpha codes, corresponding common and scientific names, and habitat association category for bird species used in multivariate analyses (Chesser et al. 2021, Pyle and DeSante 2021). Grassland habitat association categories are derived from Vickery et al. 1999.

Four-letter alpha code	Common names	Scientific names	Habitat association
AMGO	American Goldfinch	*Spinus tristis*	Generalist
AMRO	American Robin	*Turdus migratorius*	Generalist
BEVI	Bell's Vireo	*Vireo bellii*	Generalist
BHCO	Brown-headed Cowbird	*Molothrus ater*	Grassland Facultative
BOBO	Bobolink	*Dolichonyx oryzivorus*	Grassland Obligate
BRTH	Brown Thrasher	*Toxostoma rufum*	Generalist
COGR	Common Grackle	*Quiscalus quiscula*	Generalist
COYE	Common Yellowthroat	*Geothlypis trichas*	Grassland Facultative
DICK	Dickcissel	*Spiza americana*	Grassland Obligate
EAKI	Eastern Kingbird	*Tyrannus tyrannus*	Grassland Facultative
EAME	Eastern Meadowlark	*Sturnella magna*	Grassland Obligate
FISP	Field Sparrow	*Spizella pusilla*	Generalist
GRCA	Gray Catbird	*Dumetella carolinensis*	Generalist
GRSP	Grasshopper Sparrow	*Ammodramus savannarum*	Grassland Obligate
HESP	Henslow's Sparrow	*Centronyx henslowii*	Grassland Obligate
INBU	Indigo Bunting	*Passerina cyanea*	Generalist
KILL	Killdeer	*Charadrius vociferus*	Grassland Facultative
MODO	Mourning Dove	*Zenaida macroura*	Grassland Facultative
NOBO	Northern Bobwhite	*Colinus virginianus*	Grassland Facultative
NOCA	Northern Cardinal	*Cardinalis cardinalis*	Generalist
RNPH	Ring-necked Pheasant	*Phasianus colchicus*	Grassland Facultative
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	Grassland Facultative
SEWR	Sedge Wren	*Cistothorus stellaris*	Grassland Obligate
SOSP	Song Sparrow	*Melospiza melodia*	Generalist
WAVI	Warbling Vireo	*Vireo gilvus*	Generalist
WIFL	Willow Flycatcher	*Empidonax traillii*	Generalist
YEWA	Yellow Warbler	*Setophaga petechia*	Generalist

Bird Community Response to Disturbance

Bird species richness was highest in unburned units, regardless of bison presence, in comparison to burned units without bison (Figure 3). Contrastingly, there was no difference between richness within unburned units, and burned units that contained bison. This contrasted with our hypothesis of intermediate disturbance levels resulting in the highest richness. Consistent with previous research, lower richness within freshly burned prairie may indicate that grassland birds are sensitive to recent fire, or that fire is discouraging generalist species that prefer habitat with a component of woody vegetation (Zimmerman 1997, Bruckerhoff et al. 2020). Interestingly, this loss in richness was not observed in units with a combination of burned and grazed prairie, suggesting that bison disturbances may compensate for the species richness losses caused by recent prescribed fire. Previous research has shown mixed results of the impacts of grazing (both cattle and bison) on bird richness with and without prescribed fire (Zimmerman 1997, Coppedge et al. 2008, Bruckerhoff et al. 2020, Sliwinski et al. 2020). Overall, these mixed results highlight that the impacts of these disturbances on bird richness are often dependent on the intensity, frequency, and site-specific qualities within a given system.

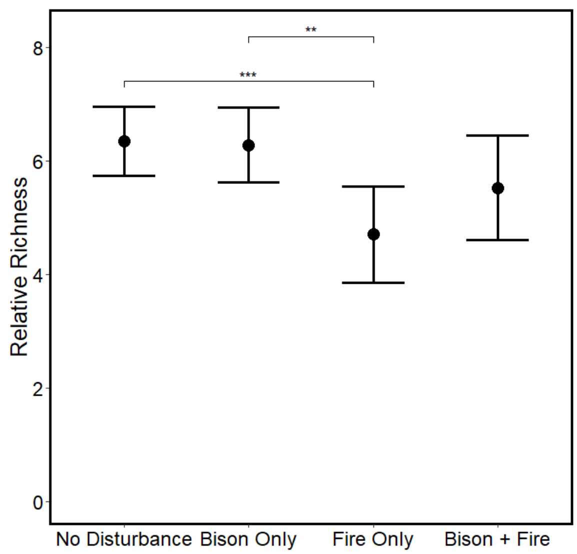

Figure 3. Plots of predicted values from GLM of categorical disturbance type and grassland bird richness. Significant pairwise comparisons using Bonferroni corrected p-values are indicated with asterisks as follows (“*” = p<0.05, “**” = p<0.01, “***” = p<0.001).

Bird community composition varied by nine percent with respect to within-year disturbance types (Figure 4). Additionally, bird community composition varied across eight vegetation structure variables, which are plotted as vectors in Figure 5. Based on these vectors, the x axis of Figure 4 represents a gradient from high to low vegetation density and height, while the y axis represents a gradient of high thatch, grass, and woody cover, to high forb and bare ground cover. Both survey year and preserve accounted for minimal but significant differences in bird community composition, with survey year and preserve (Figure 6) accounting for about one percent of variation each.

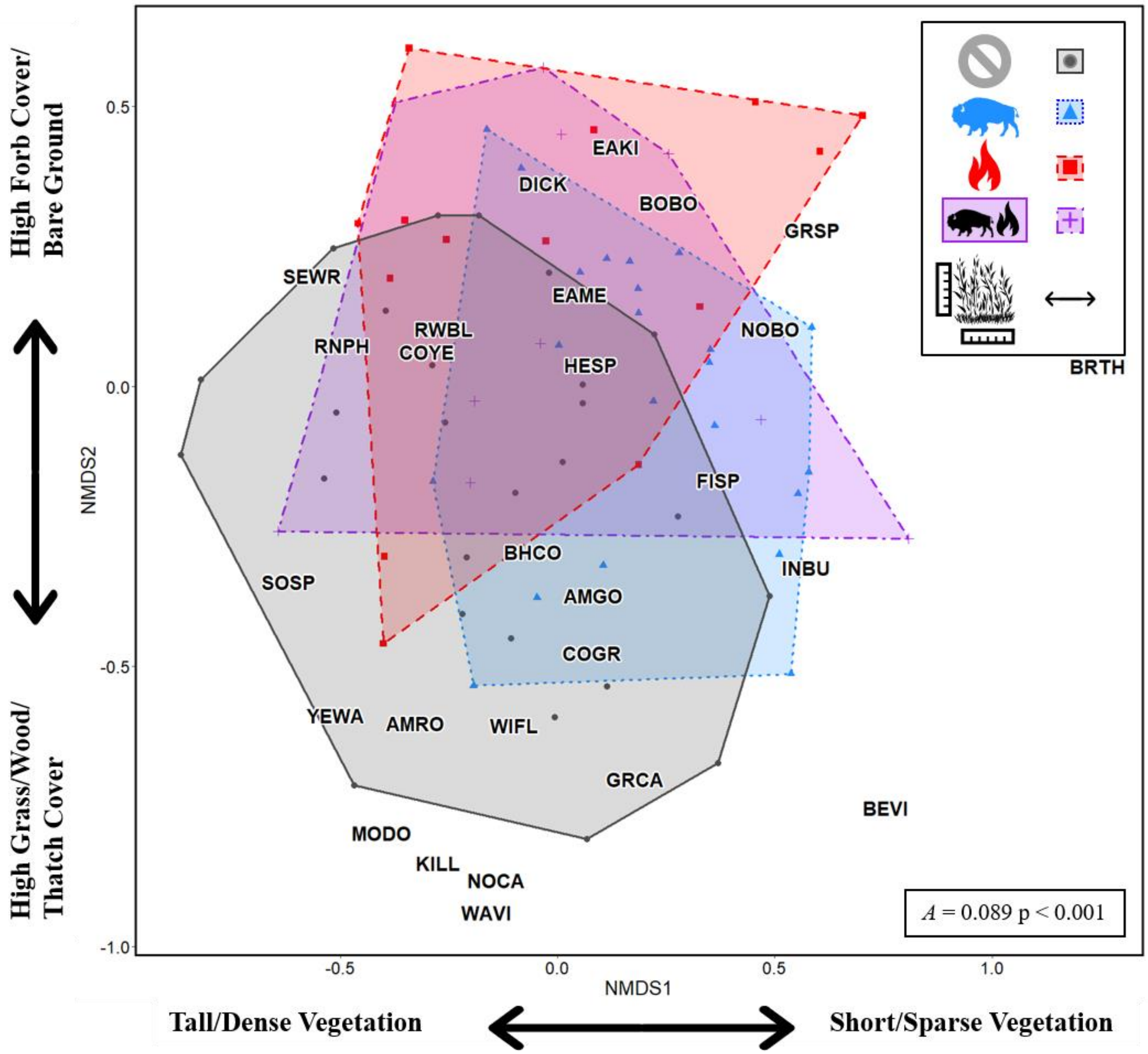

Figure 4. Visualization of grassland bird community composition via non-metric multidimensional scaling (NMDS) plots. Stress = 0.2303905 on k = 2 dimensions. Data points represent individual bird communities at survey plots per year, with more similar bird communities being closer in two-dimensional ordination space. Hull outlines are drawn to connect data points of the same disturbance type, but these outlines do not represent actual statistical borders in two-dimensional space. Bird species are represented by four-letter codes and species within a given region of the plot represent higher relative abundances within that disturbance type. Multi-response permutation procedure A statistic and corresponding p-values are reported for difference in disturbance type. Axis are labeled with a gradient of shifting vegetation structure derived from Appendix S1: Figure S1.

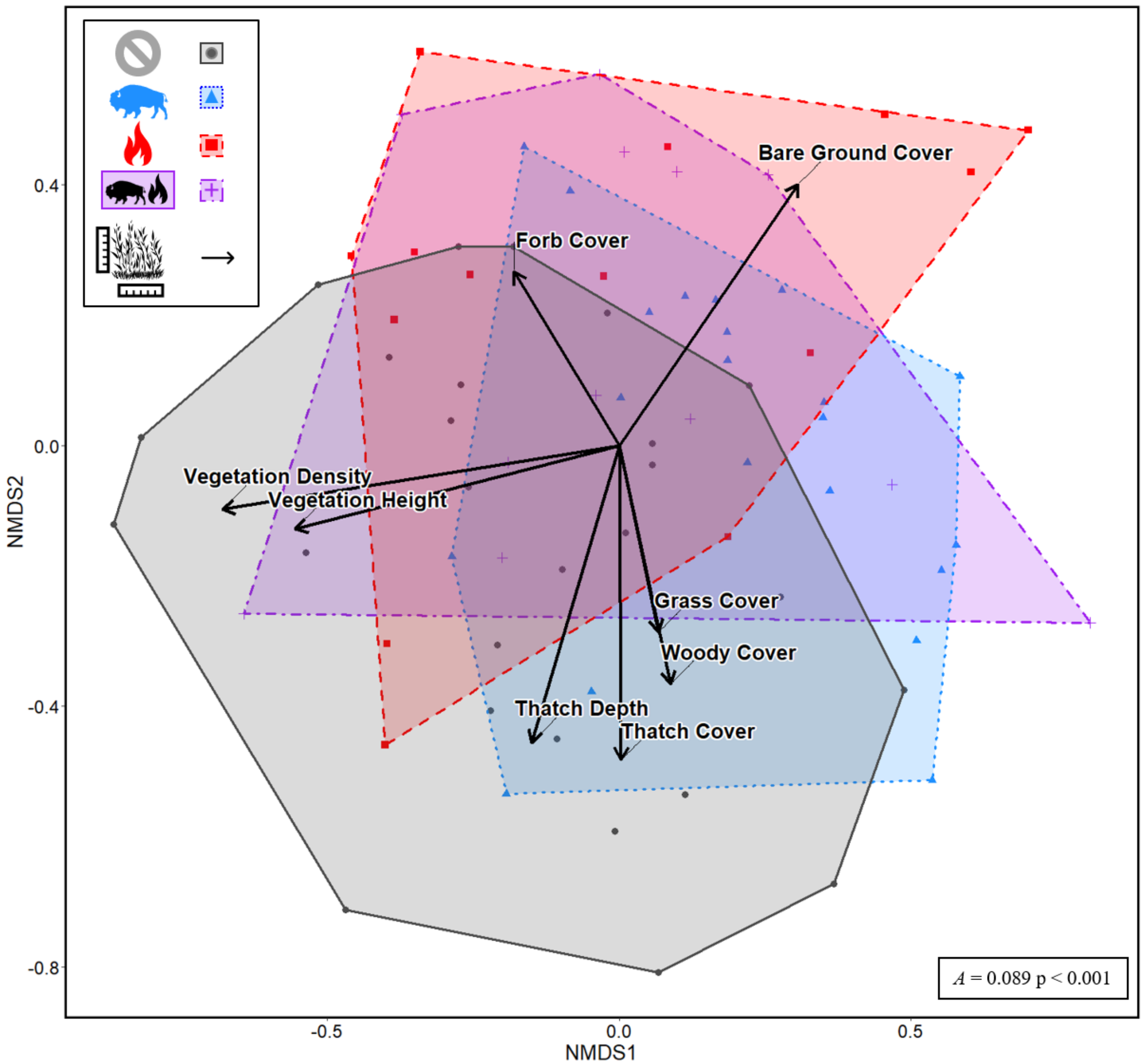

Figure 5. Visualization of grassland bird community composition via non-metric multidimensional scaling (NMDS) plots with the same data and hulls as described in Figure 3. Vegetation structure variables are represented as vectors, with vectors representing the direction of most rapid change in a variable and length corresponding to variable correlation to the ordination plot. Multi-response permutation procedure *A* statistic and corresponding p-values are reported for the difference in disturbance type

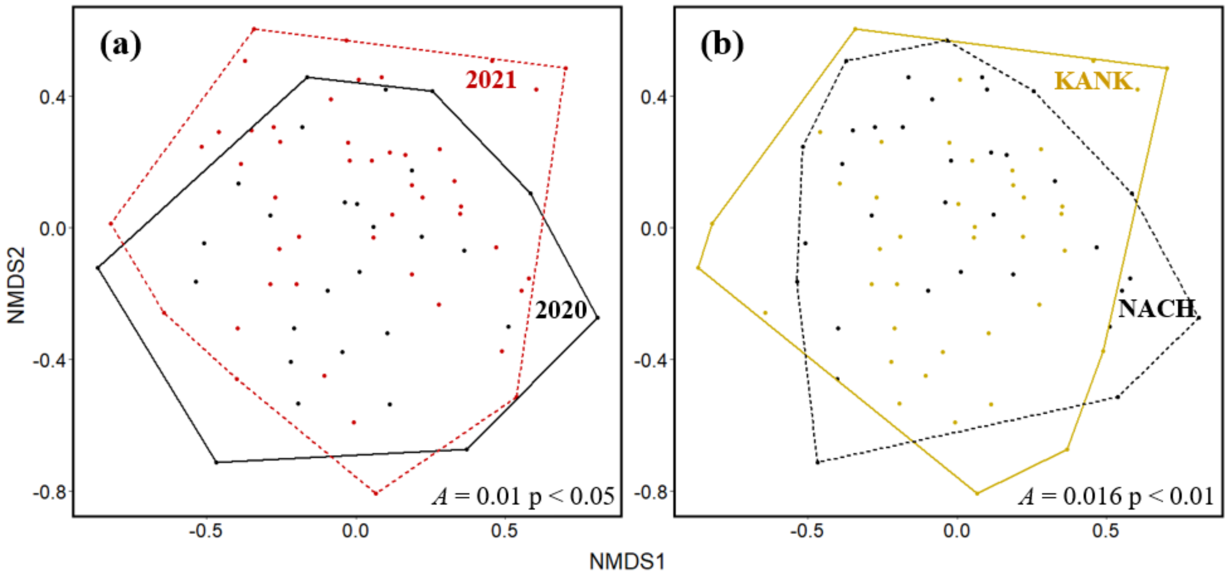

Figure 6. Visualization of grassland bird community composition via non-metric multidimensional scaling (NMDS) plots with the same data as described in Figures 2-3. Hull outlines are drawn to connect data points of the same sampling year (a) and preserve (b). Preserve plot labels (b) are identified as follows: KANK (Kankakee Sands), NACH (Nachusa Grasslands). Multi-response permutation procedure *A* statistic and corresponding p-values are reported for each NMDS plot.

Grassland bird communities clearly shift in the presence of bison and fire, as well as changes in vegetation structure, reflecting species-specific habitat preferences (Figure 4, 5) Generalist bird species are selecting areas with higher levels of woody vegetation, grass, and thatch cover, reflective of prairie habitat that has not been grazed or burned recently. Additionally, specialized obligate species are selecting areas with higher levels of forb cover and/or bare ground, reflective of prairie habitat impacted by fire and bison disturbances. Many grassland breeding birds were present across multiple management units, while species such as Dickcissel, Bobolink, Eastern Kingbird, Grasshopper Sparrow, and Northern Bobwhite preferred areas with bison and fire disturbances exclusively (Figure 4). Contrastingly, generalist species like American Robins, Song Sparrows, and Yellow Warblers preferred areas without recent disturbance, reflecting a preference for habitat with shrubland components (Figure 4). Comparatively, clear shifts in bird community composition based on differences in habitat structure have been observed in other grassland focused studies (Ahlering and Merkord 2016, Duchardt et al. 2018, Silva and Fontana 2020, Sliwinski et al. 2020). Previous studies at Nachusa Grasslands have shown no impact of bison or fire disturbance on grassland bird richness or relative detection frequencies immediately following bison reintroduction (Herakovich et al. 2021). Similar to studies with higher grazing (cattle and bison) intensities or longer established grazing disturbances, our study indicates that bison disturbances are now impacting bird communities at these preserves, highlighting the presence of a time-lag in bird response to grazing that was hypothesized by Herakovich et al. 2021 (Fuhlendorf et al. 2006, Ahlering and Merkord 2016, Fagre 2018).

Species-specific Responses to Disturbance

Dickcissel abundance was twice as high in disturbed areas on average (Figure 7); they were most abundant in recently burned sites, with a gradual decrease with years since fire (Table 2, Figure 8). Dickcissels had lower abundances in areas with high bare ground or grass cover. Interpreting this as a direct relationship is counterintuitive, as grazing and fire disturbances are often associated with higher levels of bare ground (Coppedge and Shaw 2000, Fuhlendorf et al. 2006, Elson and Hartnett 2017). Grass cover was correlated with forb cover in the study sites, so this may be an indication that Dickcissels are preferring areas with higher forb cover. Previous research has shown that both bison grazing and prescribed fire can reduce the cover of dominant grass species (e.g. *Andropogon gerardii*, *Sorghastrum nutans*) to allow for a more diverse assemblage of forb species to grow (Towne et al. 2005, Bowles and Jones 2013, Elson and Hartnett 2017).

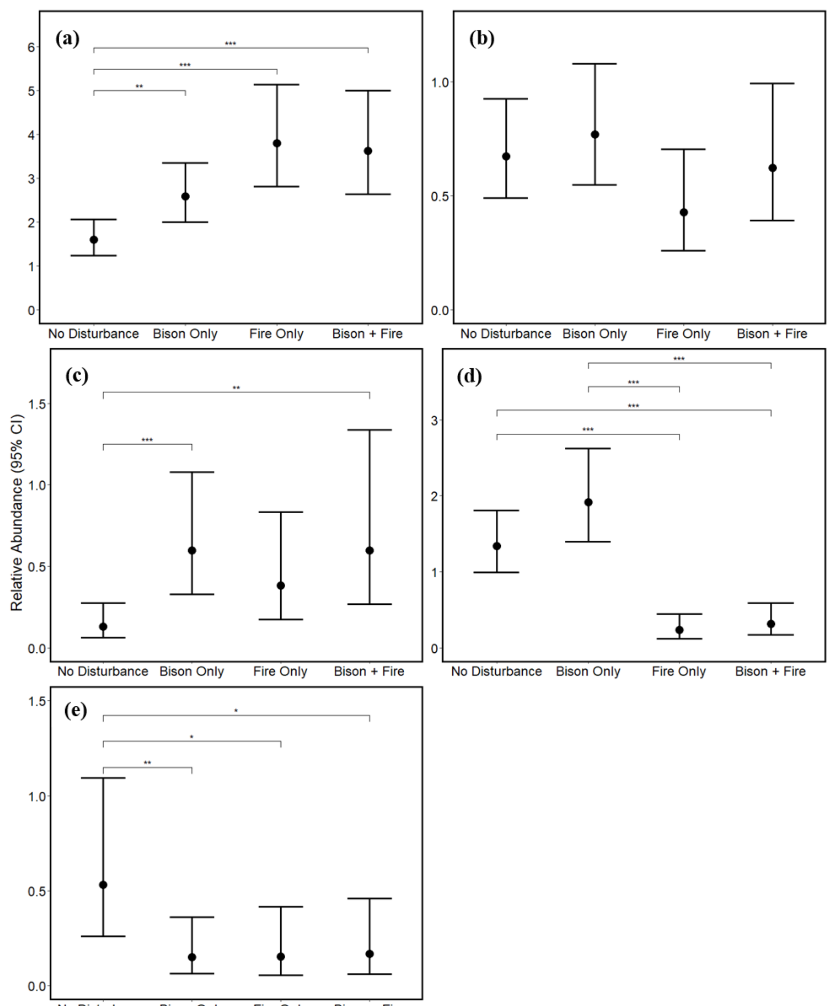

Figure 7. Plots of predicted values from GLMMs of categorical disturbance type and grassland bird abundance for five focal species: Dickcissel (a), Eastern Meadowlark (b), Grasshopper Sparrow (c), Henslow's Sparrow (d), and Sedge Wren (e). Significant pairwise comparisons using Bonferroni corrected p-values are indicated with asterisks as follows ("*" = p<0.05, "**" = p<0.01, "***" = p<0.001).

Table 2. Results from top GLMMs for each focal grassland bird species. Beta estimates, standard errors (SE) and p-values are listed for corresponding fixed effects. All beta estimates are on the log scale. Variance and standard deviations (SD) are listed for corresponding random effects. P-values are indicated with asterisks as follows (“*” = p<0.05, “**” = p<0.01, “***” = p<0.001).

	Relative Abundance				
Fixed effects:	**Dickcissel**	**Eastern Meadowlark**	**Grasshopper Sparrow**	**Henslow’s Sparrow**	**Sedge Wren**
Intercept	2.208^{***} (0.323)	0.294 (0.220)	0.400 (0.431)	-0.633^{*} (0.256)	-2.535^{***} (0.702)
Years Since Fire	-0.113^{***} (0.018)			-0.090^{**} (0.029)	-0.094^{*} (0.039)
Bison Presence	-0.131 (0.137)		0.734^{**} (0.250)	0.012 (0.282)	
Restoration Age	-0.016 (0.010)				-0.057^{*} (0.028)
Proportion of Bare Ground	-0.961^{*} (0.457)	-2.470^{***} (0.728)		-2.543^{**} (0.811)	-4.531^{**} (1.745)
Proportion of Grass Cover	-0.586^{*} (0.269)			0.547 (0.311)	2.612^{***} (0.628)
Proportion of Thatch Cover	-0.516 (0.402)		-2.225^{**} (0.734)		
Visual Obstruction Reading	-0.565 (0.344)	-1.245^{**} (0.455)	-3.521^{***} (0.746)		4.354^{***} (0.679)
Years Since Fire X Bison Presence	-0.070^{*} (0.033)			0.190^{**} (0.063)	
Random effects:					
Year:Preserve:Plot	0.098 (0.313)	0.091 (0.301)	0.558 (0.747)	0.451 (0.672)	0.646 (0.804)
Julian Date	0.071 (0.266)	0.032 (0.180)			0.276 (0.525)
Model Statistics:					
Residual Degrees of Freedom	380	409	409	406	383
Log Likelihood	-695.7	-449.0	-356.8	-516.8	-311.0
Akaike Inf. Crit.	1,415.4	907.9	723.6	1,049.6	639.9
Bayesian Inf. Crit.	1,463.0	928.1	743.8	1,081.8	675.7

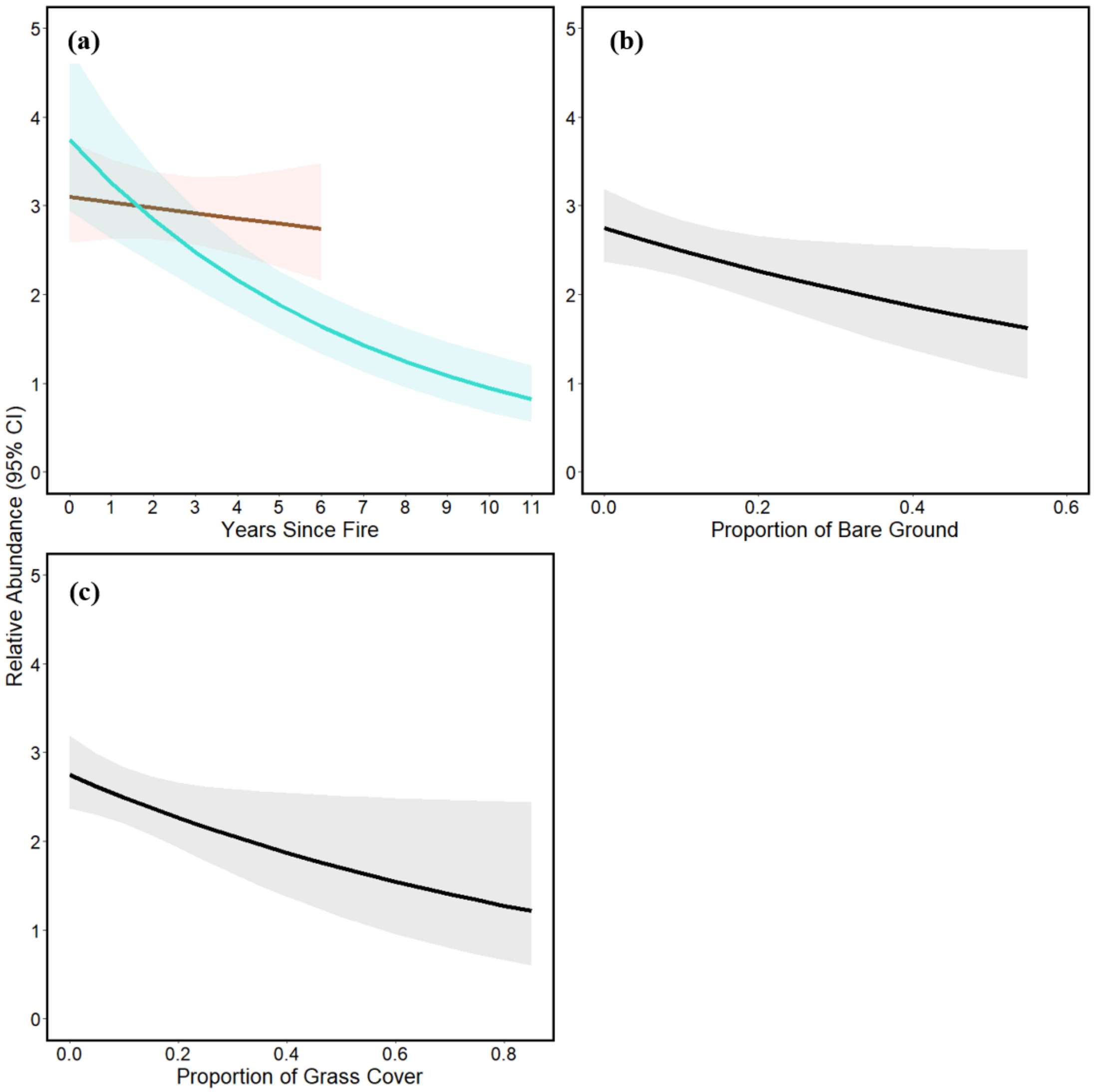

Figure 8. Plots of predicted values of significant variables from Dickcissel abundance top GLMM: years since fire in different bison management units (a), proportion of bare ground (b), and proportion of grass cover (c).

Top regression models also revealed evidence for pyric herbivory impacting Dickcissels (fire*bison interaction). Dickcissels exhibited a preference for recently burned areas with a decrease in abundance as years since fire increased (Figure 8). This relationship was mediated by the presence of bison; Dickcissel abundance decreased at a slower rate with years since fire in bison units. These results differ slightly from previous literature that suggest Dickcissels prefer areas one year after a prescribed burn, and either prefer management units without bison or have no preference regarding bison disturbances (Powell 2006, Herakovich et al. 2021).

Eastern Meadowlarks showed no preference for different disturbance regimes, but preferred areas with shorter, thicker vegetation cover (Table 2, Figure 9). This is largely consistent with previous literature that has shown this species selects for prairie habitat with moderate vegetation height, mixed with grass, forbs, and thatch (Hull 2000, Geller et al. 2004).

However, previous studies have also shown mixed results with respect to bison and fire disturbance impacts, with some studies indicating lower abundances in recently burned areas and higher abundances in moderately grazed prairie, and others indicating no significance (Zimmerman 1992, Hull 2000, Geller et al. 2004, Powell 2006). These results in combination with past literature show that Eastern Meadowlarks have consistent vegetation preferences, but the impact of grazing and fire disturbances on this species is variable. Future research may be warranted to uncover the potential causes for this variation in response to disturbances.

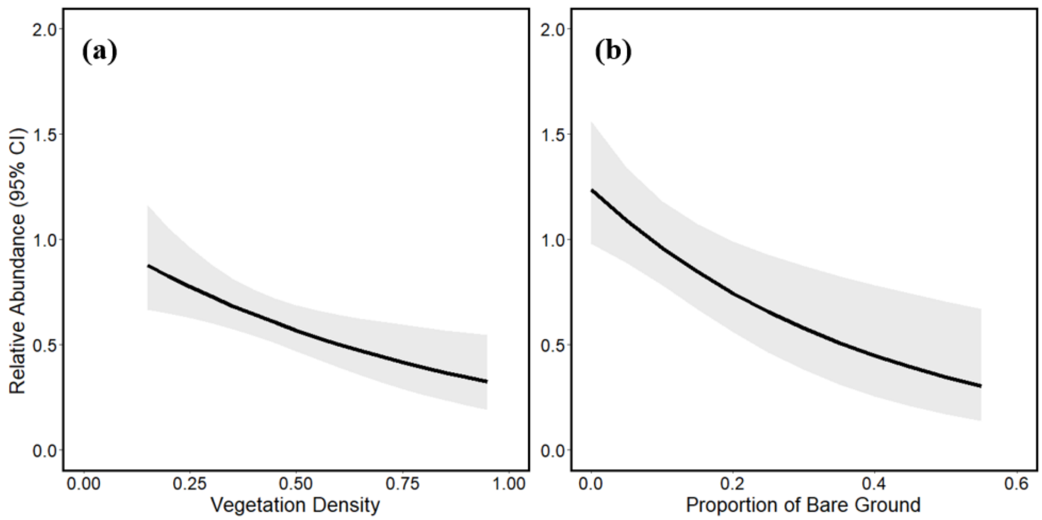

Figure 9. Plots of predicted values of significant variables from Eastern Meadowlark abundance top GLMM: visual obstruction reading (a) and proportion of bare ground (b).

Grasshopper Sparrows were four times more abundant in disturbed areas on average in comparison to areas without bison or fire (Figure 7) and three times more abundant in bison units compared to non-bison units, regardless of fire history (Table 2). Plots with dense vegetation saw a 97 percent decrease in Grasshopper Sparrow abundance compared to plots with low vegetation density. Similarly, Grasshopper Sparrow abundance decreased by 89 percent along a gradient of low to high thatch cover (Table 2, Figure 10). This is similar to other studies that found Grasshopper Sparrows showed an affinity for bison units and were abundant in prairie habitat with less dense vegetation and less thatch cover (Fuhlendorf et al. 2006, Powell 2006).

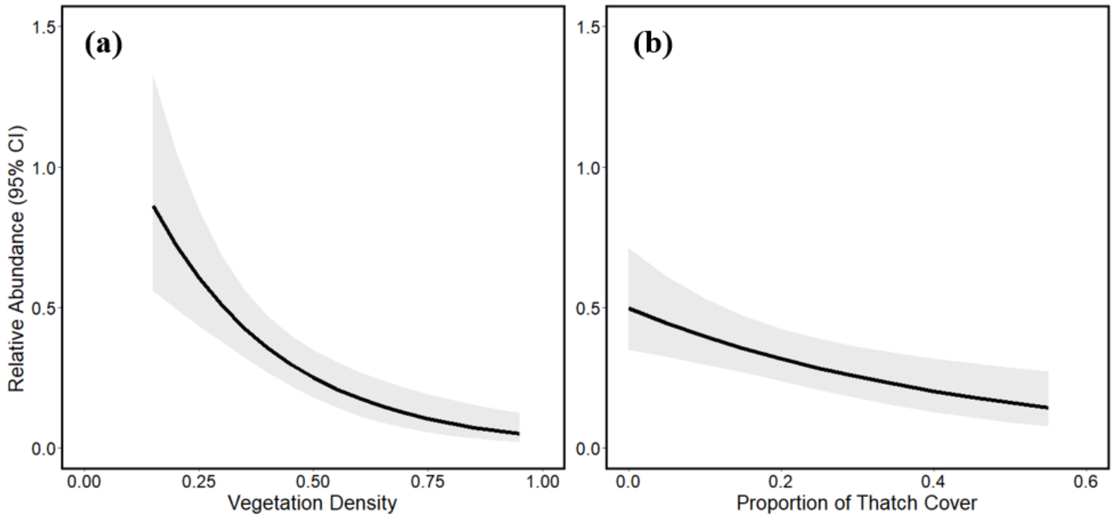

Figure 10. Plots of predicted values of significant variables from Grasshopper Sparrow abundance top GLMM: visual obstruction reading (a) and proportion of thatch cover (b).

Henslow's Sparrow abundance were at near zero values in plots that were burned prior to the survey year (Figure 7). Henslow's Sparrow abundance decreased 92 percent when bare ground reached its highest levels in comparison to areas with no bare ground (Table 2, Figure 11). Pyric herbivory impacted Henslow's Sparrows such that their abundance increased at a faster rate with increased years since fire within bison units compared to non-bison units (Figure 11). Henslow's Sparrow preference of unburned prairie habitat has been well documented in the literature in various tallgrass prairies (Herkert 1994b, 2002, Fuhlendorf et al. 2006, Powell 2006, Hovick et al. 2015). This species requires a layer of dead plant litter (thatch) within its breeding habitat, which is continuously removed by periodic prescribed burning. Contrasting to our findings, Henslow's Sparrows in western prairies have much lower abundances with prairie grazed by bison, with no observed interactive relationship between bison and fire (Powell 2006).

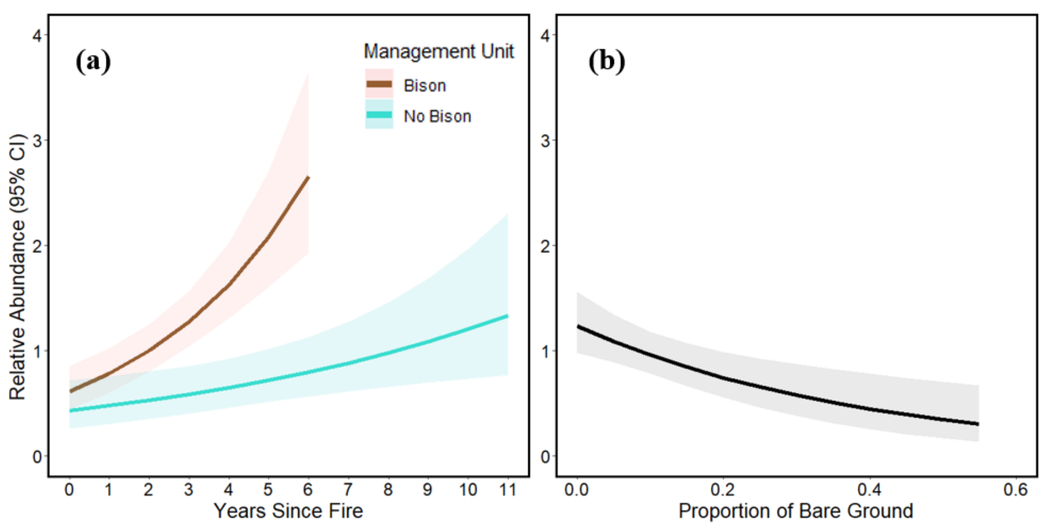

Figure 11. Plots of predicted values of significant variables from Henslow's Sparrow abundance top GLMM: years since fire in different bison management units (a) and proportion of bare ground (b).

We offer some potential mechanisms that may explain Henslow's Sparrow response to fire in areas with and without bison. First, we know that bison and their interactive grazing patterns with fire (pyric herbivory) increase the abundance of invertebrates within these preserves and others, which may offer an additional food source for Henslow's Sparrows in comparison to areas with similar fire histories, but no bison (Swengel 2001, Joern 2005, Engle et al. 2008, Doxon et al. 2011, Hosler et al. 2021). Secondly, large herbivores, such as bison, can create reduced fuel loads, reducing prescribed fire uptake in grassland systems (Leonard et al. 2010, Blackhall et al. 2017, Starns et al. 2019). Bison graze areas that have recently been burned, removing plant material through grazing, therefore removing some fuel for future fires. Subsequent fires may not burn as well within heavily grazed areas, allowing some thatch to remain within an area that was burned. At our study sites, thatch is more common and its cover increases more rapidly in the absence of fire within bison units in comparison to management units without bison, lending credence to this explanation (Figure 12). Lastly, it is important to note that the highest abundances of Henslow's Sparrows occur in prairie that has not been burned for four to seven years. These large fire return intervals only occurred within Kankakee Sands, highlighting the importance for varied fire return intervals within preserves.

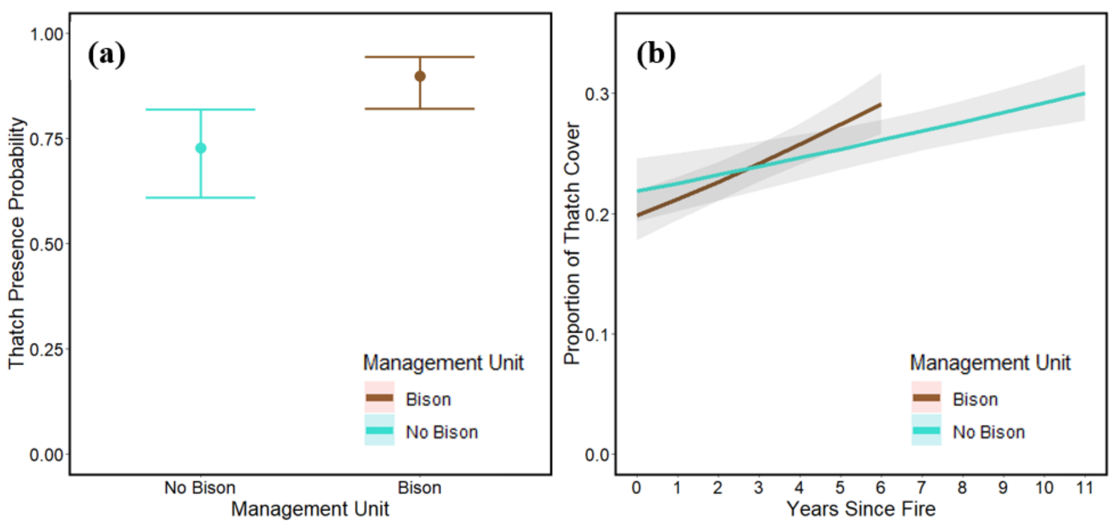

Figure 12. Plots of predicted values from additional GLMM analyses of bison presence and thatch presence probability (a) and proportion of thatch cover in different management units on a gradient of years since fire (b).

For categorical disturbance types, Sedge Wren abundance was higher within undisturbed areas than in units that were burned and/or had bison (Figure 7). For continuous management variables, Sedge Wrens were slightly less abundant as years since fire and restoration age increased. Sedge Wrens were more abundant in areas with dense vegetation and more grass cover, and less abundant with more bare ground cover. Overall, vegetation structure variables had stronger impacts than management variables for Sedge Wrens, with vegetation density exhibiting the strongest relationship on the abundance of this species (Table 2, Figure 13). Previous studies are mostly consistent with these results, showing Sedge Wrens prefer dense vegetation and wetter grassland habitat (Schramm et al. 1986, Dechant et al. 2002). These preferences for undisturbed prairie show the importance of maintaining areas of tallgrass prairie without grazers and with longer fire return intervals to ensure disturbance-intolerant species have refugia. This is especially important in isolated eastern tallgrass prairies, where connected or nearby undisturbed grassland habitat may be completely absent.

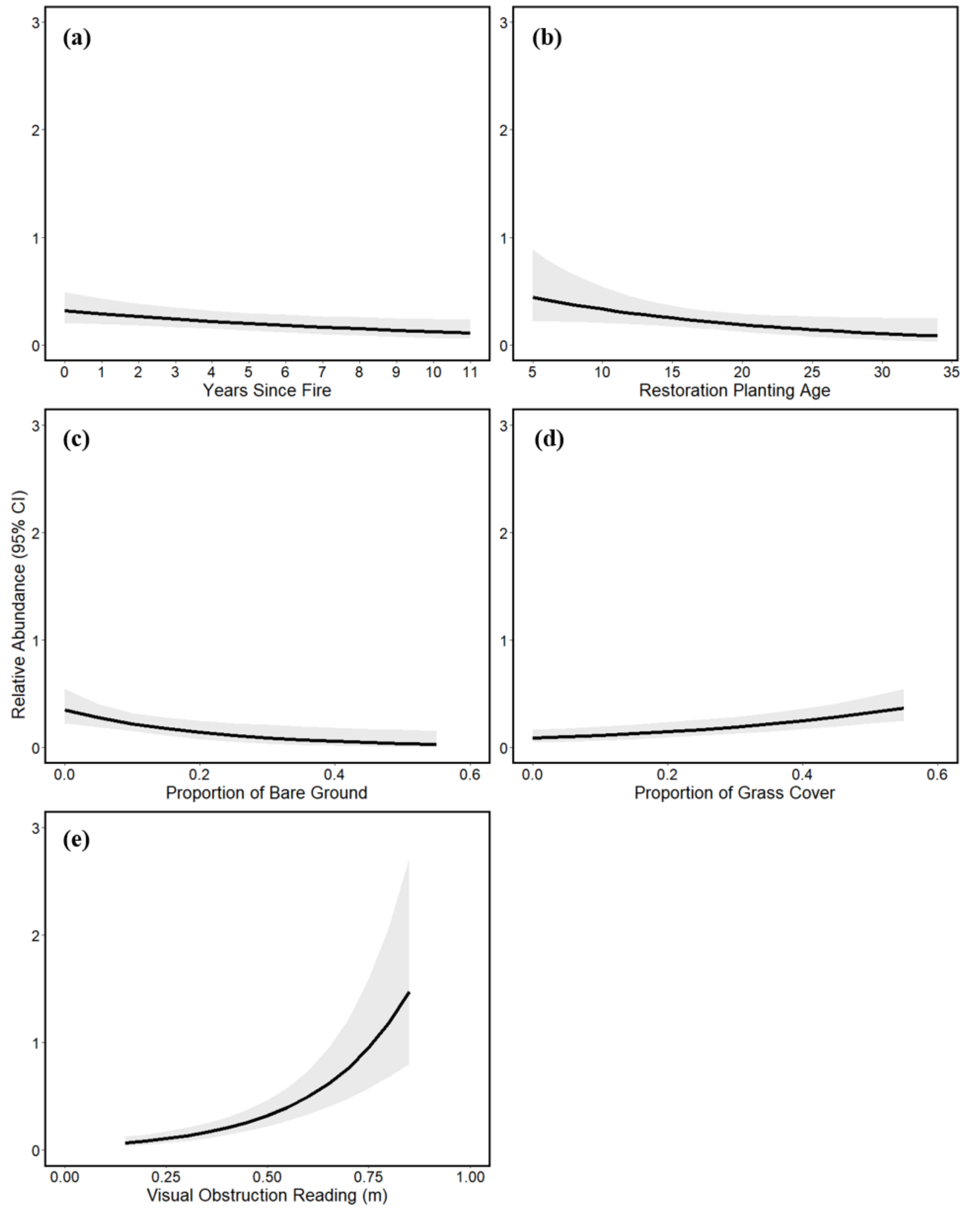

Figure 13. Plots of predicted values of significant variables from Sedge Wren abundance top GLMM: years since fire (a), restoration planting age (b), proportion of bare ground (c), proportion of grass cover (d), and visual obstruction reading (e).

Science Delivery Activities

The culmination of the completion of this project has resulted in a number of science delivery activities. Manager-relevant reports were submitted to preserve managers at both project sites following data collection after both survey years. Additionally, presentations have been made at a number of local and regional conferences to disseminate the findings from this project to both research and management focused people and groups. A number of outreach activities have also been conducted within the local community at the university and project sites. For example, the student researcher presented at an outreach event for local grade school students to learn about growing STEM fields and career opportunities of the future. The student researcher was also able to attend and lead a educational birding tour at Nachusa Grasslands annual Autumn on the Prairie Festival 2022, an event that had been canceled the two previous years due to the Covid-19 pandemic. A masters thesis was successfully defended in April and the student's thesis has been made publicly accessable via ProQuest and NIU's Huskie Commons repository. Lastly, select chapters from the thesis have been submitted for publication in the Journal of Applied Ecology. The student will continue through the editing and submittal process until the article is accepted and published in a peer-reviewed scientific journal. A complete list of relevant of science delivery activities has been provided in Appendix B.

Conclusions

Key Findings

Our results reveal that bison and prescribed fire disturbances can have strong effects on bird community composition and species abundances in restored tallgrass prairies, although not all species respond positively to these disturbances. Disturbances from bison, fire, and their combined interaction had a stronger impact on bird community composition than interannual variation or preserve location. The species-specific responses of five focal species further highlight the importance of heterogenous disturbance, as they widely varied in their responses to different disturbance regimes. Additionally, species-specific results showed preference for certain vegetation structure characteristics, aligning with life history preferences of these grassland bird species. Overall, vegetation structure had the largest impact on bird abundances, with grazing and fire disturbances having larger impacts than restoration planting age and spatiotemporal factors. These results highlight the importance of applying varying levels of grazing and fire disturbance in order to provide heterogeneous vegetation structure that accommodates the life history preferences of different grassland bird species.

Previous studies have shown that cattle grazing and fire disturbances have a strong impact on vegetation structure, which in turn impacts grassland birds (Coppedge et al. 1998a, 2008, Fuhlendorf et al. 2006, Powell 2008, Hovick et al. 2015). Fewer studies have focused on the specific impacts of bison grazing and the potential interactive impact of bison and fire disturbances on grassland birds (Powell 2006, Wilkins et al. 2019, Boyce et al. 2021, Herakovich et al. 2021, Kaplan et al. 2021). This is the second study to look at bison and fire impacts on grassland birds in eastern tallgrass prairies, and the first to look at impacts on abundances and community composition across multiple preserves in this region (Herakovich et al. 2021). Overall, our results show stronger impacts of vegetation structure on grassland bird abundances than management, highlighting that the impact of disturbance is often indirect, through the medium of vegetation (Guiden et al. 2021). Additionally, our study has shown the importance of studying the interactive impact of bison and fire disturbances on grassland bird species where these disturbances are applied in combination. Specifically, this pyric herbivory may be playing a role in Dickcissel and Henslow's Sparrow abundances that has not been previously described. As managers continue to reintroduce native herbivores, like bison, to tallgrass prairies and other ecosystems, it will be important to study the impact these keystone species exhibit on flora and fauna through disturbances. In combination with the application of prescribed fire in these fire-adapted systems, native grazers may interact with and accentuate or dampen the impact of fire across the landscape. Our research highlights the important implications that these historical disturbance regimes have on the future restoration and conservation of rare tallgrass prairie ecosystems and the declining grassland birds that use this habitat to breed.

Future Research

This research adds to the body of literature on bison and prescribed fire impacts on grassland birds, while also suggesting future avenues for research. Further research is required to unpack the potential mechanisms behind the interactive impact of bison and fire on bird species such as Dickcissel and Henslow's Sparrow. We offered a few potential mechanisms behind this relationship, such as, increased food sources and bison impacting prescribed fire uptake and continuity. Future studies analyzing the diets of these species, as well as the physics of prescribed fire uptake in bison grazed prairie versus ungrazed prairie may provide better insight into these mechanisms.

The importance of habitat heterogeneity mediated by varying disturbance regimes is highlighted in our results and supported by other studies (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009, Hovick et al. 2015). However, our study does not encompass all levels of preserve size, connectivity, or disturbance seen within prairie systems. The absence or low occurrence of certain grassland obligate species like Bobolink and Upland Sandpiper (*Bartramia longicauda*) indicate that there may be missing pieces of the mosaic of different disturbance regimes and subsequent micro-habitats. Upland Sandpipers have been shown to prefer highly grazed areas, and it is possible that these high grazing patches are not being achieved at these preserves (Fuhlendorf et al. 2006, Powell 2006, Sandercock et al. 2015, Ahlering and Merkord 2016). Consideration of increasing habitat area and applying different combinations of disturbance may be warranted to attract these species. Future studies investigating bison disturbances may look to incorporate studying bison impacts on grassland birds at more drastic levels of grazing intensity. Additionally, larger grassland obligate species like Northern Harrier (*Circus hudsonius*) and Short-eared Owl (*Asio flammeus*) were observed sparingly during surveys, but our survey techniques were not adequate for sampling the large habitat ranges of these species. Future studies may consider incorporating additional methods to study these species of concern as well.

Implications for Management and Policy

The future of grassland birds depends on the conservation and restoration of preserves that create, connect, and protect vital prairie habitats. In eastern tallgrass prairies, where tallgrass prairie habitat has largely been removed from the landscape, these preserves are even more critical for the conservation of species found locally (Herkert 1994a, Robertson et al. 1997). As two of the largest tallgrass prairie preserves in the region, Kankakee Sands and Nachusa Grasslands set the precedent for what tallgrass prairie restoration projects can accomplish regionally. As managers continue to reintroduce native herbivores, like bison, to tallgrass prairies and other ecosystems, it will be important to study the impact these keystone species exhibit on flora and fauna through disturbances. In combination with the application of prescribed fire in these fire-adapted systems, bison may interact with and accentuate or dampen the impact of fire across the landscape. Our results highlight the importance of pyric herbivory for two grassland obligate species, Dickcissels and Henslow's Sparrows. The specific propensity for Henslow's Sparrows to select grazed prairie that has not been burned for 4-7 years may provide a recommendation for managers at Nachusa Grasslands to consider larger fire return intervals within certain management units for the benefit of this species. Additionally, our results highlight the need for ungrazed and unburned refugia within this mosaic of bison and fire disturbance, especially for sensitive species like Sedge Wrens. Overall, maintaining management units with different levels and frequency of bison and fire disturbance is critical for creating micro-habitats for species-specific breeding requirements. Specific management strategies could be used to target certain species, but a mosaic of different disturbance regimes appears to be the best strategy for the grassland bird community as a whole at these sites. These are all important implications that these historical disturbance regimes have on the future restoration and conservation of rare tallgrass prairie ecosystems and the declining grassland birds that use this habitat to breed. The continued variable application of bison and fire on these preserves, along with the continued expansion and adaptation of evidence-based restoration efforts, will help to provide strongholds for grassland bird conservation within this region.

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Appendix A: Contact Information for Key Project Personnel

- Principal Investigator (Student):
    - Antonio Del Vallé
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- Principal Investigator (Advisor):
    - Holly P. Jones
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Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

- Scientific Articles
  - Del Valle, A., Guiden, P.G., Jones, H.P. 2022. Grassland Bird Responses to Bison and Prescribed Fire in Restored Tallgrass Prairies. Journal of Applied Ecology. In Review.
- Conference Abstracts & Presentations (* indicates presenter)
  - Del Valle, A.*, Jones, H.P. 2022. Grassland bird responses to bison and prescribed fire disturbances at Nachusa Grasslands and Kankakee Sands. Northern Illinois University, Department of Biological Sciences, Thesis Defense Presentation.
  - Del Valle, A.*, Jones, H.P. 2022. Grassland bird responses to bison and prescribed fire at Nachusa Grasslands and Kankakee Sands. Nachusa Grasslands Science Symposium. Invited Presentation & Abstract.
  - Del Valle, A.*, Jones, H.P. 2022. Grassland bird responses to bison and prescribed fire disturbances in Illinois and Indiana tallgrass prairies. Illinois Chapter of The Wildlife Society Annual Meeting. Oral Presentation & Abstract.
  - Del Valle, A.*, Jones, H.P. 2022. Birds on the prairie: grassland bird response to bison and prescribed fire in Illinois and Indian tallgrass prairie. Midwest Fish and Wildlife Conference. Oral Presentation & Abstract.
  - Del Valle, A.*, Jones, H.P. 2021. Grassland breeding bird response to bison and prescribed fire in eastern tallgrass prairies. Garden Club of Evanston, Garden Club of America Scholar Program. Invited Presentation.
  - Del Valle, A.*, Jones, H.P. 2021. Grassland bird responses to bison disturbances at Nachusa Grasslands and Kankakee Sands. Nachusa Grasslands Science Symposium. Invited Poster & Abstract.
  - Del Valle, A.*, Jones, H.P. 2021. Grassland bird responses to bison disturbances in tallgrass prairies in Illinois and Indiana. Midwest Ecology and Evolution Conference. Poster & Abstract.
  - Del Valle, A.*, Jones, H.P. 2021. Grassland bird response to bison and prescribed fire disturbances in restored tallgrass prairie. Midwest Fish and Wildlife Conference. Oral Presentation & Abstract.
  - Del Valle, A.*, Jones, H.P. 2020. Bison, Birds, and Prairies: How do reintroduced bison impact breeding birds in eastern tallgrass prairies?. Northern Illinois University, Department of Biological Sciences Seminar. Oral Presentation.
- Graduate Thesis
  - Del Valle, A. 2022. Grassland bird responses to bison and prescribed fire disturbances at Nachusa Grasslands and Kankakee Sands. Northern Illinois University, Department of Biological Sciences. Master of Science Thesis.
- Outreach (* indicates presenter)
  - Del Valle, A.* 2022. Birding on the edge. The Nature Conservancy, Nachusa Grasslands, Autumn on the Prairie Festival. Invited Outreach Tour.
  - Del Valle, A.* 2022. Ecosystem restoration. Northern Illinois University, Teen STEM Café: “Jobs of the Future”. Invited Presentation & Outreach Activity

  - Del Valle, A.*, Jones, H.P. 2021. Grassland bird conservation in North America and research in restored tallgrass prairies. Northern Illinois University, BIOS 457/557 Biology of Birds and Mammals. Invited Lecture.
- Manager-relevant Reports
  - Del Valle, A. 2021. The Nature Conservancy, Annual Research Report.
  - Del Valle, A. 2020. The Nature Conservancy, Annual Research Report.

Appendix C: Metadata

Metadata will be made available following the data products, curation, and data-use policy (see below) from the project Data Management Plan.

Data products, curation, and data-use policy:

Raw data will be freely available upon publication or following a 2-year embargo. Data from specific publications and associated R code will be deposited in Dryad. All data from the project will be deposited in DataOne together at the end of the funding period. During the grant period, we will make data available upon request as long as project personnel be offered authorship as appropriate on publications.